**US Army Corps
of Engineers**
Waterways Experiment
Station

Aquatic Plant Control Research Program

Influence of *Pistia stratiotes* Plant Quality on Fecundity and Egg Distribution of the Biological Control Agent *Spodoptera pectinicornis*

by   G. S. Wheeler, T. D. Center, T. K. Van,
      Agriculture Research and Education Service

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Final report

US Army Corps of Engineers
Waterways Experiment Station

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AREA OF RESERVATION · 2.7 sq km

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Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32406. The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Center for Aquatic Plant Research and Technology (CAPRT), Dr. John W. Barko, Director. Mr. Robert C. Gunkel, Jr., was Assistant Director for the CAPRT. Program Monitors during this study were Mr. Timothy Toplisek and Ms. Cheryl Smith, HQUSACE.

This report was prepared by Drs. G. S. Wheeler, T. D. Center, and T. K. Van, United States Department of Agriculture - Agriculture Research Service (USDA-ARS), Aquatic Plant Control Research Center, Fort Lauderdale, Florida.

This investigation was performed under the supervision of Dr. Alfred F. Cofrancesco, Jr., Leader, Biomanagement Team, APCRP, EL; Dr. Edwin Theriot, Chief, Aquatic Ecology Branch, EL; Dr. Conrad Kirby, Chief, Ecological Research Division, EL; and Dr. John Harrison, Director, EL.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Robin R. Cababa, EN.

This report should be cited as follows:

1   Introduction

Insect fecundity is one of the most important components determining the population dynamics of a species and is influenced by many biotic factors (Courtney and Kibota 1990, Leather 1994). Although the potential fecundity of a species may be dramatically compromised by many factors (Leather 1988), it can be increased with greater female body size as demonstrated in several groups of insects, for example, scales (McClure 1980), planthoppers (Denno and McCloud 1985), lepidoptera (Hough and Pimentel 1978, Morris and Fulton 1970, Gunn and Gatehouse 1985), and aphids (Whitham 1978). Increased fecundity also has been found when lepidopteran larvae were fed relatively high quality diets (Taylor 1984, Taylor and Sands 1986, Taylor and Forno 1987). Insects of either pest or beneficial species fed food of relatively high nutritional quality may have increased fecundity resulting in outbreak populations (Myers 1987).

The leaf selected for oviposition by many herbivorous insects determines the leaf in which the developing larvae initiate feeding and complete development (Crawley 1983). The monophagous biological control agent *Spodoptera pectinicornis* (Hampson) (Lepidoptera: Noctuidae) which oviposits and feeds on leaves of the aquatic plant waterlettuce *Pistia stratiotes* L. (Habeck and Thompson 1994) were studied for the purpose of this report. This species oviposits egg masses and at least some of the first instars penetrate the leaf directly below the egg mass (Habeck and Thompson 1994). Larval growth and development rate of this species is significantly improved by feeding on fertilized host plants. Considering the relatively high incidence of parasitism that occurs in other lepidopteran herbivore species associated with *P. stratiotes* (Knopf and Habeck 1976) and the potential increased exposure to these natural enemies because of the extended development (Damman 1987, Stamp and Bowers 1990) on low nutritional food, the location of the eggs on the host plant may be of critical importance for the success of this species.

The correlation between oviposition preference and larval performance has been demonstrated in only a few examples and, in general, has not held up to scrutiny (Wiklund 1975, Thompson 1988). Most of these studies have compared oviposition and performance on different species of potential host plants, whereas a few have suggested that the ovipositional preference within the plant microhabitat may also be as important

(Whitham 1980, Craig, Itami, and Price 1989). As *P. stratiotes* plant quality can vary dramatically from plant to plant or from leaf to leaf within the same plant, oviposition preference for particular leaves or microhabitats on a leaf can influence larval performance. A previous study (Wheeler, Van, and Center 1998) indicated that *S. pectinicornis* females oviposited preferentially on plants fertilized at a relatively high level compared to plants fertilized at a low level. Foliar nitrogen is frequently identified as a performance-limiting nutrient in herbivorous insects (Mattson 1980). Moreover, the generally low nitrogen levels of *P. stratiotes* were found to limit the performance of *S. pectinicornis*. Therefore, it was predicted that *S. pectinicornis* eggs would be laid most often on the leaves containing the highest nitrogen content. In this study, the impact of larval nutrition on adult fecundity and the distribution of eggs laid on the host plant is assessed.

2   Materials and Methods

Plant Collections and Tissue Analysis

Pistia stratiotes plants (4-5 leaves per plant) were field collected and grown at two fertilizer levels to determine the effect of dietary nutrients on female egg production. These treatments consisted of *P. stratiotes* plants cultured in 64 L pots (0.16 m^2 surface area) inside a 3- x 2-m cage at a relatively high fertilizer (5 ppm nitrogen with Peter's 15-5-15 and 2 ppm Fe, flushed and changed weekly) and low fertilizer rate (0.25 ppm nitrogen with Peter's 15-5-15 and 0.1 ppm Fe, flushed and changed weekly). Three plants and four plants were grown in each pot for the high and low fertilizer treatments, respectively, and each treatment was replicated four times. The plants were grown for four months until they completely covered the water surface of the pots in which they were grown. All fully expanded leaves ($n = 3$) were cut as needed for the experiments and refrigerated. Percent nitrogen, phosphorus, and potassium contents were determined on a dry weight basis. Leaf digests were conducted by a Kjeldahl method (Hach et al. 1987). Nitrogen content was determined by the ammonia-selective electrode method, phosphorus by the ascorbic acid method, and potassium by atomic absorption chromatography (Greenberg, Clesceri, and Eaton 1992). Standard reference materials (tomato leaves; National Institute Standard Technology (NIST)) were analyzed as controls and values were adjusted for percent recovery.

Insects

Neonate *S. pectinicornis* larvae were collected from the laboratory colony which had been in culture for six months (about six generations) without infusion of wild genotypes. Each larva was fed leaves (1-4 position) from either the low or the high fertilized plants until pupation in petri dishes (150 x 25 mm) lined with moistened filter paper and sealed with parafilm. Single pairs of adult males and females, either from the low or high (for both $n = 21$) treatments were fed a mixture of water and honey (3:1) in cylindrical cages (13 cm in diameter by 35 cm in length). Each cage contained a single *P. stratiotes* plant from the high fertilized

treatment whose roots were placed in a pondwater-filled jar (3.8 L) located on moist filter paper. Plants were changed and the egg masses or solitary eggs were counted daily.

Data Collection and Analysis

Data were collected on leaf nitrogen, phosphorus, and phosphate content, pupal fresh biomass for each sex, adult longevity, the number of egg masses, eggs per mass, solitary eggs, and unlaid eggs determined after dissection and examination of the dead females. Also noted was the leaf position, leaf surface, and the day in which eggs were laid. All analyses were conducted with SAS/PC (SAS Institute, Inc. 1988). The results of leaf percent nitrogen, phosphorus, and phosphate were analyzed on individual leaves, from the inner to the outer positions. Overall means of these elements were compared (a priori) with least squared means. A regression analysis was used to determine the effect of fertilizer treatment on leaf nitrogen, phosphorus, and potassium content from the inner to the outer leaves. Regression slopes were compared with a covariate analysis. Pupal biomass and adult longevity were analyzed by one-way analysis of variance (ANOVA) for each sex with fertilizer treatment as the main effect. The number of egg masses, eggs per egg mass, solitary eggs, and total eggs produced were analyzed by one-way ANOVAs. The influence of female pupal biomass on total egg production was analyzed by linear regression. To determine if the location of egg masses or solitary eggs were influenced by fertilizer treatment, day (age of female), leaf position (leaves 1-12), or leaf surface (upper vs. lower), the data (square-root transformed) were analyzed by a repeated measures ANOVA. Data were clumped by days (1-2, 3-4, and 5-6) and leaf positions (1-4, 5-8, and 9-12) to reduce the frequency of zero cells. Both leaf position and adult age were analyzed as linear and polynomial variables. Specific means of percent of the total egg masses and solitary eggs were analyzed by one-way ANOVAs followed by a priori Ryan's Q mean comparison test (probability $P = 0.05$).

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3 Results

Plant Quality

Overall, the nitrogen content (Least squared means, ± SE (standard error)) of the high fertilizer treatment leaves (3.36 ± 0.05 percent dry weight) was higher than that of the low treatment (0.87 ± 0.05 percent). The inner leaves from the high fertilized *P. stratiotes* plants had the highest nitrogen content which decreased toward the outer leaves (Figure 1). The nitrogen content of the low fertilized plants also decreased in the outer leaves, but the slope of this line was significantly less than that of the high fertilized plants. Similarly, the overall phosphorus content of the high fertilizer treatment leaves was higher (0.75 ± 0.01 percent) than that of the low treatment leaves (0.46 ± 0.01 percent). The phosphorus content of the inner high treatment leaves was highest and decreased toward the outer leaves. However, the opposite occurred in the low fertilizer treatment plants, where the phosphorus content was lowest in the inner-most leaves and increased toward the outer leaves. Potassium content of the high treatment (5.29 ± 0.09 percent) leaves overall was higher than that of the low treatment (4.09 ± 0.09 percent). Potassium levels increased significantly with leaf position only in the low fertilizer treatment.

Pupal Biomass, Adult Longevity, and Egg Production

The biomass of male and female pupae that developed from larvae fed the high fertilized plants were significantly greater compared with those fed the low fertilized plants (Table 1). Longevity of the adult females was slightly shorter on the high fertilized plants; however, male longevity did not differ between the two treatments (Table 1). Of the initial number of adult pairs ($n = 21$), 20 and 19 pairs produced egg masses in the high and low treatments, respectively. In addition to egg masses, 14 and 17 adult pairs produced solitary eggs in the high and low treatments, respectively.
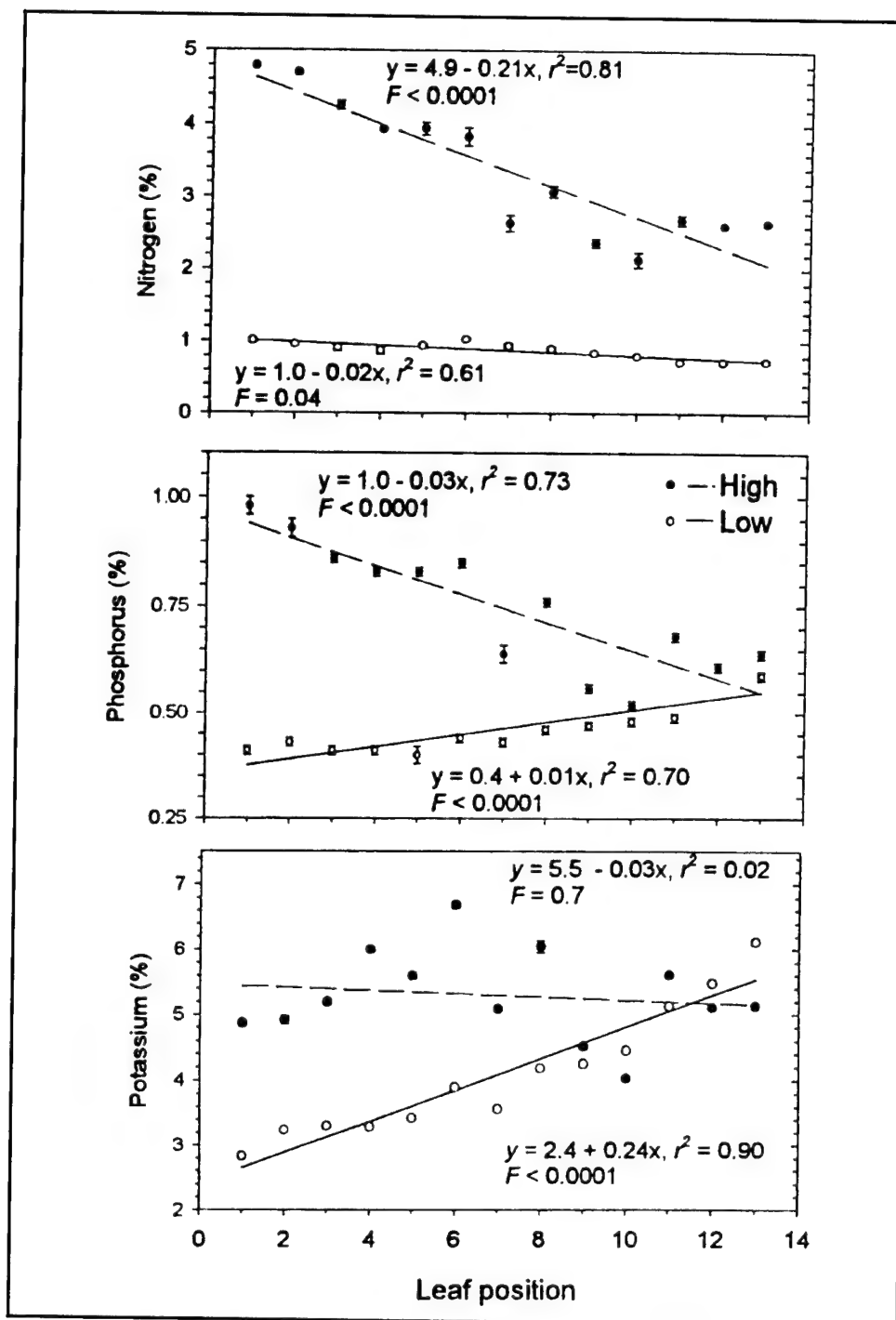
Figure 1. Percent nitrogen, phosphorus, and potassium (dry weight) of
P. stratiotes leaves from plants fertilized at high or low rates. Overall,
foliar nitrogen ($F_{1,74} = 773.0$, $P < 0.0001$), phosphorus ($F_{1,74} = 170.11$,
$P < 0.0001$), and potassium ($F_{1,74} = 144.49$, $P < 0.0001$) levels were
higher in the high than in the low fertilizer leaves. Nitrogen levels
decreased more rapidly in the high treatment from the inner to the
outer leaves than in the low ($F_{1,74} = 121.8$, $P < 0.0001$). The slopes of
phosphorus levels across leaf positions also differed significantly
($F_{1,74} = 170.1$, $P < 0.0001$). Potassium levels increased significantly
with leaf position only in the low treatment leaves

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Table 1
Mean (± SEM) *S. pectinicornis* Pupal Biomass, Adult Longevity, and Egg Production from Larvae Fed Leaves of Plants Fertilized at High and Low Rates

Treatment	n	Sex	Biomass (mg)	SEM	Range	F value	Degrees of Freedom (df)	P value
High	20	female	80.3	3.2	48.6–110.8	3.16	1,37	0.08
Low	19		70.2	4.8	40.2–104.2			
High	20	male	59.9	2.1	43.6–82.7	20.68	1,37	< 0.0001
Low	19		45.6	2.4	25.2–70.3			
			Longevity (d)					
High	20	female	3.8	0.3	1–6	3.33	1,37	0.08
Low	19		4.6	0.4	2–7			
High	20	male	4.6	0.3	2–7	0.78	1,37	0.78
Low	19		4.4	0.4	1–7			
		Egg masses/female						
High	20	15.3		1.8	6–35	2.10	1,37	0.16
Low	19	12.1		1.3	3–22			
		Egg masses/female/d						
High	20	4.3		0.48	1.3–8.8	8.13	1,37	0.007
Low	19	2.7		0.28	1.2–5.7			
		Eggs/mass						
High	20	43.6		1.9	7–187	0.70	1,37	0.40
Low	19	41.3		2.1	6–176			
		Total solitary eggs/female						
High	14	99.7		20.0	8–306	0.06	1,29	0.80
Low	17	108.2		25.7	10–383			
		Total solitary eggs/female/d						
High	14	24.8		4.6	2.0–52.3	0.32	1,29	0.58
Low	17	21.1		4.7	2.8–76.6			
		Total eggs/female						
High	20	835.9		74.1	355–1,694	2.19	1,37	0.15
Low	19	683.5		75.5	292–1,526			
		Total eggs/female/d						
High	20	251.94		18.8	106.0–374.7	13.47	1,37	0.0011
Low	19	160.86		16.4	73.0–305.2			

Generally, the larvae that were fed the higher fertilized plants produced moths with greater fecundity (Table 1). Although the difference in total fecundity per female between the treatments was marginally significant ($P = 0.15$), the difference in total fecundity per female per day was highly significant ($P = 0.0011$). Because the females from the low fertilizer treatment survived longer, when these data are expressed as a rate (i.e., per day), the number of egg masses produced per female per day and the total number of eggs produced per female per day were significantly greater in adults from the high fertilizer treatment. Moreover, total egg production was influenced by the biomass of the pupae reared from either diet, where the females that emerged from pupae with greater biomass produced significantly more eggs when the larvae were fed either the high or the low fertilized plants (Figure 2). Differences in the slopes of these lines were not significant.
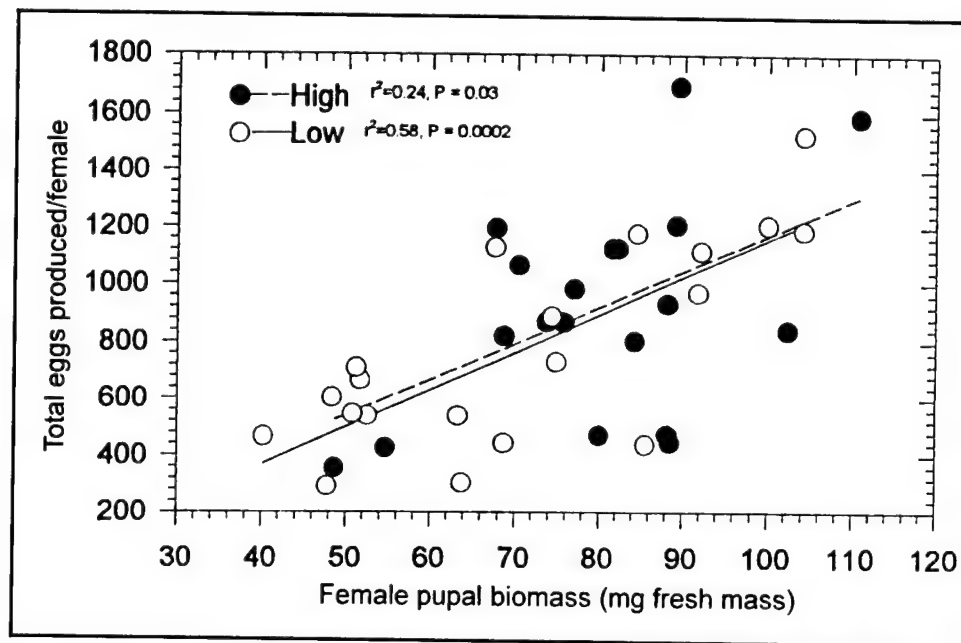
Figure 2. Total number of eggs produced by *S. pectinicornis* females as a function of female pupal biomass (mg) fed as larvae leaves of *P. stratiotes* plants fertilized at high and low levels. The slopes of the regression equations for the high (y = -29.5 + (10.8x)) and low (y = -47.7 + (10.4x)) fertilizer levels did not differ significantly

Egg Location

Observations of egg mass positions indicated that they were typically placed in a small depression formed by the removal of leaf hairs by the ovipositing female. (This should be developed further with a scanning electron microscope of the egg mass depression.) The percentages of the total number of eggs produced that were in masses, as solitary eggs or recovered from dissections of females, differed little between the fertilizer treatments (Figure 3). In both the high and the low fertilizer treatments more than 70 percent (79.5 and 72.4 percent, respectively) of the

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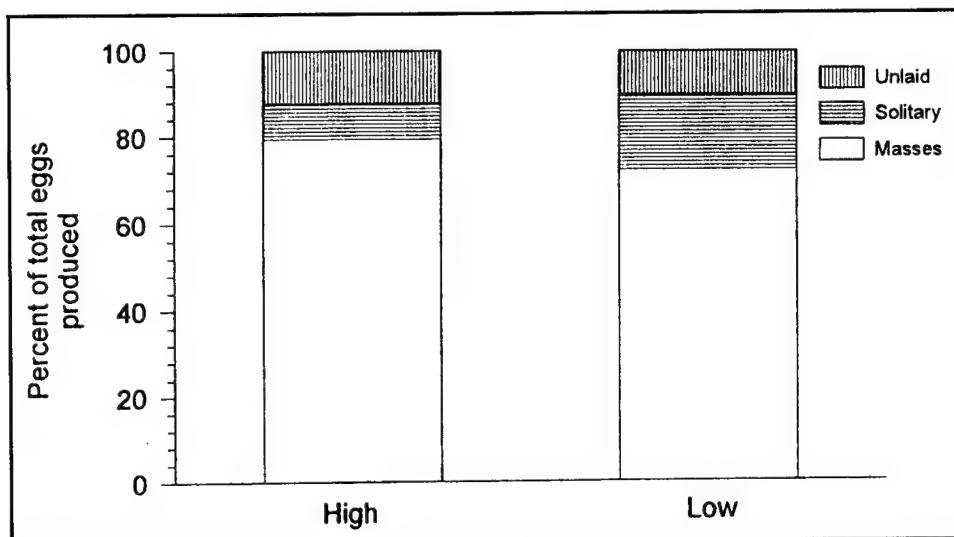
Figure 3. Percent of the total number of eggs produced that were either in masses, solitary, or counted from the dissected dead females. Results are from *S. pectinicornis* fed as larvae *P. stratiotes* fertilized at high or low rates. A significantly greater percentage of the total number of eggs were solitary in the low compared with the high fertilizer treatment ($F_{1,37} = 4.16$, $P = 0.05$)

eggs were deposited in masses. No differences occurred between the two fertilizer treatments in the percentage of eggs in masses or in the percentage of unlaid eggs that remained inside the females after death. However, a significantly greater percentage of the total number of eggs (mean ± SEM) were solitary in the low (17.3 ± 3.4 percent) compared with the high (8.3 ± 2.3 percent) fertilizer treatment. Eggs found on surfaces other than the plant (e.g., moist filter paper) comprised 4.1 percent of the total in the high and 1.6 percent in the low treatment.

Egg masses were found on leaves 1 through 12, with the majority on leaves 5 through 8 (Figure 4). Egg mass location was significantly affected by leaf position and the interaction between leaf position and fertilizer level. Significantly more eggs were laid by the high than the low fertilizer-reared females at leaf positions 9-12.

Egg mass location was significantly affected by leaf surface and day or age of the female (Figure 5). Significant interactions between both leaf position and leaf surface, and leaf position and days, indicated that the percentage of egg masses laid on different surfaces or days was not the same at different leaf positions. A greater percentage of the egg masses were laid on the lower than the upper leaf surface at all leaf positions. Furthermore, a greater percentage of the egg masses were laid during days 1 and 2 than 3 and 4, which were greater than during 5 and 6 at leaf positions 1-4 and 5-8. A greater percentage of the egg masses were laid during days 1 and 2 than all other days at leaf positions 9-12.
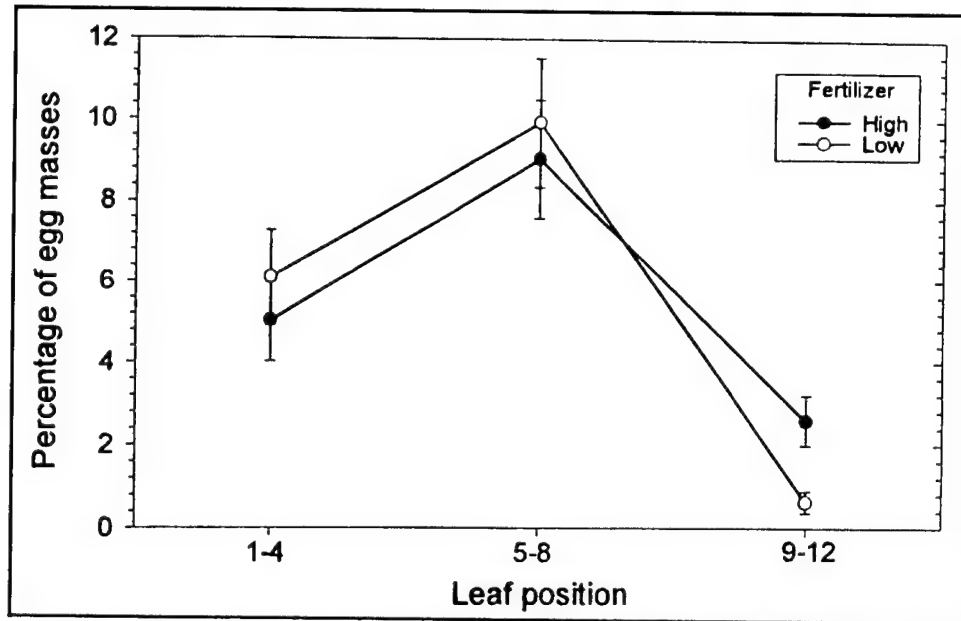
Figure 4. Average number of egg masses laid at different leaf positions by
S. pectinicornis fed as larvae leaves of *P. stratiotes* plants fertilized at
high or low rates. Egg mass location was significantly affected by leaf
position (Linear: $F_{1,38} = 51.99$, $P < 0.0001$; Quadratic: $F_{1,38} = 66.36$,
$P < 0.0001$) and the leaf position fertilizer interaction ($F_{2,76} = 3.22$,
$P = 0.0455$). Significantly more egg masses were laid by the high than
the low fertilizer treatment females at leaf positions 9-12 ($F_{1,238} = 9.58$,
$P = 0.0022$)

Egg masses were found during days 1-6 with the majority on days
1 and 2 (Figure 6). A significant day-by-leaf-surface interaction indicated
that the percentage of egg masses laid on the different surfaces was not
the same during different days. During days 1 and 2 and days 3 and 4
more egg masses were laid on the lower leaf surface; however, no differ-
ence was found during days 5 and 6.

Solitary eggs were found on all leaves, with the greatest percentage on
leaves 5-8. The distribution of solitary eggs was significantly affected
only by leaf position and the interaction between leaf position and day
(Figure 7). The greatest percentage of solitary eggs were found during
days 1 and 2 and days 3 and 4 at leaf positions 1-4 and 5-8. Neither leaf
surface nor fertilizer treatment significantly affected solitary egg
distribution.
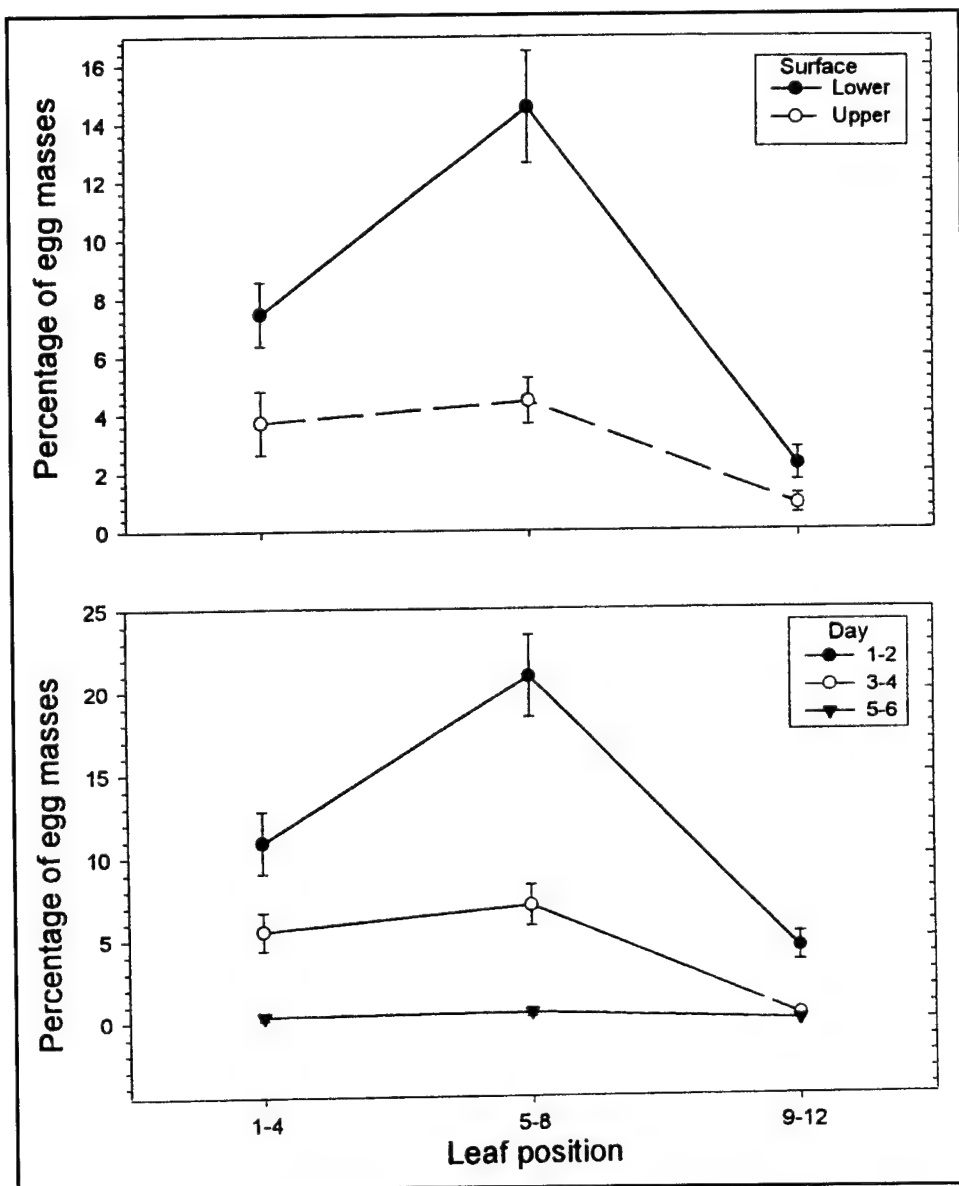
Figure 5.   Average percent of egg masses laid by *S. pectinicornis* on different leaves on either the lower or upper leaf surface or during different days. Egg mass location was significantly affected by leaf position (as in Figure 4) and leaf surface ($F_{1,38}$ = 37.93, $P < 0.0001$) and the interaction of leaf position and surface ($F_{2,76}$ = 12.2, $P < 0.0001$). A significantly greater percentage of egg masses were found on the lower leaf surface at leaf positions 1-4 ($F_{1,238}$ = 5.80, $P < 0.0168$), 5-8 ($F_{1,238}$ = 23.83, $P < 0.0001$) and 9-12 ($F_{1,238}$ = 4.63, $P = 0.0324$). Egg mass location was also significantly affected by leaf position (as in Figure 4) and day ($F_{1,38}$ = 221.38, $P < 0.0001$) and the interaction of leaf position and day ($F_{4,152}$ = 13.4, $P < 0.0001$). Significantly more egg masses were found during days 1 and 2 than 3 and 4, which was also greater than that found during days 5 and 6 at positions 1-4 and 5-8 and during days 1 and 2 than all other days at positions 9-12 according to preplanned mean comparison tests (Ryan's Q, $P = 0.05$)
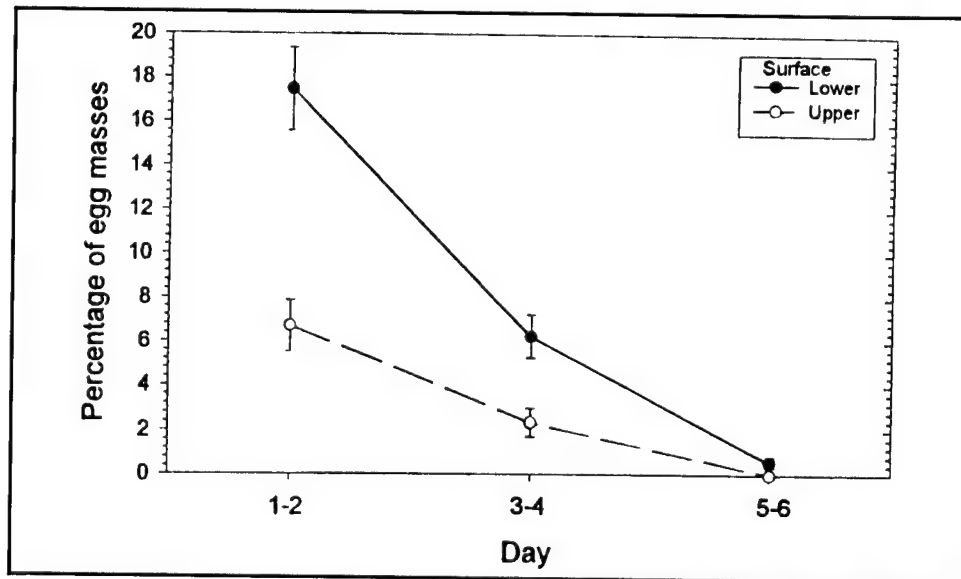
Figure 6. Average percent of egg masses laid by *S. pectinicornis* on different days and leaf surfaces. A significant day/leaf surface interaction ($F_{2,176}$ = 10.50, P < 0.0001) indicated that the percentage of egg masses laid on different leaf surfaces was not the same during different days. The percentage of egg masses laid during days 1 and 2 ($F_{1,238}$ = 23.41, P < 0.0001), days 3 and 4 ($F_{1,238}$ = 10.93, P = 0.0011) and days 5 and 6 ($F_{1,238}$ = 6.21, P = 0.0134) on the lower surface was significantly greater than those laid on the upper surface
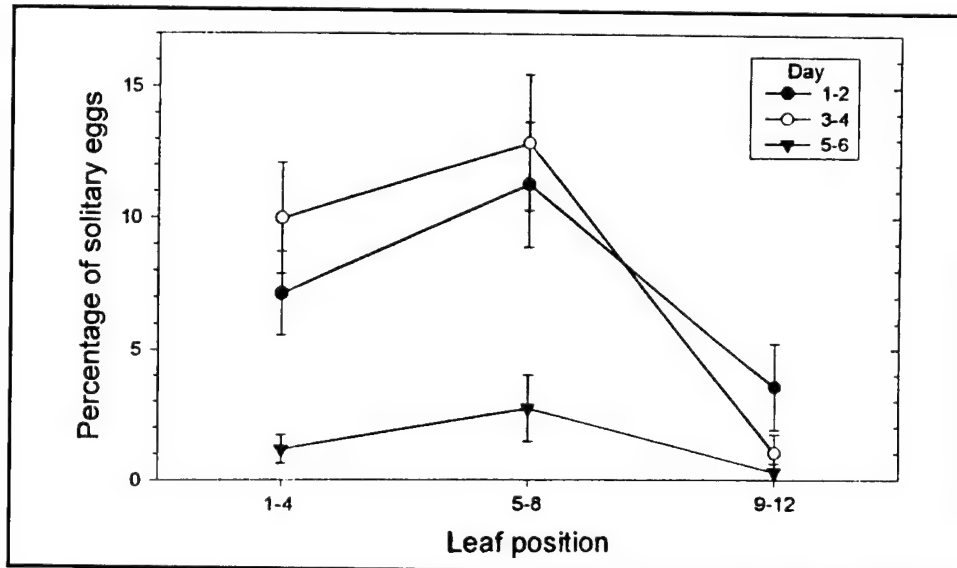
Figure 7. Average percent of solitary eggs laid by *S. pectinicornis* on different leaf positions (Linear: $F_{1,29}$ = 31.24, P < 0.0001; Quadratic: $F_{1,29}$ = 18.49, P = 0.0002) and days (Linear: $F_{1,29}$ = 19.65, P < 0.0001; Quadratic: $F_{1,29}$ = 7.14, P = 0.0122). A significant leaf position/day interaction ($F_{4,116}$ = 3.04, P = 0.0201) indicated that the percentage of solitary eggs laid on different days was not the same at different leaf positions. Significantly more solitary eggs were laid on days 1 and 2 and days 3 and 4 than on days 5 and 6 at positions 1-4 and 5-8 according to preplanned mean comparisons (Ryan's Q, P = 0.05)

4 Discussion

Plant Quality

The high fertilizer treatment significantly increased the nitrogen, phosphorus, and potassium levels of the *P. stratiotes* leaves compared with the low fertilizer treatment. Furthermore, the plants grown in the high fertilizer treatment concentrated greater amounts of nitrogen (1.8 times) and phosphorus (1.5 times) in the inner leaves compared with the outer leaves. Although a significant increase (1.4 times) in inner-leaf nitrogen occurred in the low fertilized plants, the actual amount of the increase was relatively small (0.7 - 1.0 percent) and was probably of minimal nutritional value for the insects. Previous results indicated that an increase in foliar nitrogen from 1.8 to 2.6 percent significantly decreased larval development time by 30 percent or by about 6 days. Considering the 0.3 percentage point increase in nitrogen of the inner leaves of the low fertilizer treatment, no such decrease in development time would be expected in larvae fed these leaves.

Typically foliar nitrogen, because of its central role in the health, growth, and reproduction of insects, is considered to be of critical importance potentially limiting herbivore performance (Mattson 1980). Little is known about the required levels of other foliar elements like phosphorus and potassium for insect nutrition (Mattson and Scriber 1987), although phosphorus may be important for larval growth of *Spodoptera exempta* (Janssen 1994). However, the importance of these plant macronutrients for insect nutrition may be secondary, where plants grown in low fertilizer conditions are not as nutritious in terms of proteins, lipids, digestible carbohydrates, and other nutrients.

As would be expected, the nitrogen, phosphorus, and potassium levels decreased in the outer leaves of the high fertilizer treatments. However, phosphorus and potassium levels increased in the outer leaves of the low fertilizer treatments. As plant growth may have been limited under these low nitrogen conditions, phosphorus and potassium may not have been depleted as was nitrogen in the outer leaves. Similar shifts in the balance of plant components have been documented with changes in the level of nitrogen fertilizer (Marschner 1986).

Fecundity

Larval consumption of relatively high fertilizer *P. stratiotes* plants increased total female egg production per day. Because the females from the high treatment had shorter longevity (by about one day) than those from the low treatment, the females from the high fertilizer treatment had significantly greater rates of egg production. However, relatively few egg masses were produced during the extra day. Otherwise, the only significant difference between the treatments in the number of egg masses found was at leaf positions 9-12, where more egg masses were laid by high fertilizer females. Moreover, larger females emerged from the larvae fed the high fertilized plants ($P = 0.08$), and larger females in general from both treatments produced significantly more eggs than did smaller females. Thus, although the difference in total egg production between the two treatments was marginally significant ($P = 0.15$), the increase may be of biological significance. These conclusions are supported by evidence of increased fecundity with increased body size in other lepidoptera species, for example the gypsy moth (Hough and Pimentel 1978), another *P. stratiotes* herbivore *Samea multiplicalis* (Taylor 1984) when fed *Salvinia molesta* Mitchell, *S. exempta* (Gunn and Gatehouse 1985) and *Pannolis flammae* (Leather 1984). However, as suggested (Leather 1988), the relationship between body size and fecundity may be very complex as many other factors such as adult nutrition and flight activity can influence fecundity.

A previous report (Suasa-ard 1976) suggested that this species produces an average of 94 eggs per egg mass, with each female producing 4-5 egg masses and a total of 665.9 eggs. The results of the present study indicate a somewhat higher fecundity. This higher fecundity may have resulted due to the use of insects from a different genotype, larvae fed high nitrogen plants, or the dissection of dead females and the counting of the remaining eggs. The overall fecundity between the two studies was similar; however, the greatest differences were in the numbers of egg masses and eggs per egg mass produced per female, where the present study found 12.1 - 15.3 egg masses and 41.3 - 43.6 eggs per egg mass compared with 4-5 egg masses and 94.3 ± 50.9 eggs per egg mass. It might be suspected that different genotypes were tested, even though the insect populations were both from the same general source (Thailand), as the two studies were separated by more than 20 years. A possible genetic bottleneck may have occurred as the insects were collected and reared in quarantine and then mass reared in the study's research facility. Although the potential bottleneck was minimized by rearing the insects in quarantine for less than a generation, a reduction in genetic variability of the population undoubtedly occurred. Both studies included adult diet (Suasa-ard used a 5-percent honey syrup), and the present study frequently observed adults feeding at these sources. Whether they benefit from this nutrition in terms of increased fecundity has yet to be determined. Several other factors may have contributed to these differences and further research will be required to elucidate them.

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Egg Location

Although the occurrence of lepidoptera species ovipositing both egg masses and solitary eggs has been well known (e.g., Metcalf, Flint, and Metcalf 1962), it has rarely been described in detail. The adaptive significance of laying eggs in masses versus as solitary eggs has been reviewed (Stamp 1980, Courtney 1984), and typically species are described as laying eggs in either one or the other condition. Rarely has the distribution of both conditions within the same individual been presented from an adaptive perspective. Results suggest that the production of solitary eggs increased in females when fed plants from the low fertilizer treatment. Possibly these adult females laid a greater percentage of solitary eggs as an adaptive response to disperse the subsequent generation and thereby reduce competition among their offspring. As these adults were reared on relatively low-quality plants, the larval diet may have induced the observed change in oviposition preference.

Batch-laying lepidoptran species may utilize host plants that are relatively large or plants that typically grow in aggregations capable of supporting several individuals (Courtney 1984). While a *P. stratiotes* plant may have enough foliage to support the development of several larvae of this species, the plant is typically found in large aggregations growing in more sheltered areas of lakes and streams (Dewald and Lounibos 1990). Eggs laid in masses may be at an advantage compared with solitary eggs because of the removal of the leaf hairs below the site of egg mass oviposition, a condition not found with solitary eggs. Many first instars penetrate the leaf at this site (Habeck and Thompson 1994), thereby circumventing any protective role of the leaf hairs and tough epidermal covering. This is thought to be a primary source of larval mortality in *S. pectinicornis*, and removal of these hairs either artificially (Hoffman and McEvoy 1986) or naturally may lead to greater survival. Such advantages may not be available to the larvae hatching from solitary eggs. Additionally, egg masses are typically covered by abdominal scales from the ovipositing female (Suasa-ard 1976, Habeck and Thompson 1994), possibly to protect the eggs from natural enemies or from desiccation. Observations indicated that no such scales covered the solitary eggs, and they were thus more susceptible to these potential sources of mortality. Most egg masses were laid on the lower surface of leaves, whereas solitary eggs were laid equally on both surfaces. Although the upper surface has shorter leaf hairs, exposure to natural enemies is probably greater than on the lower surface. Solitary eggs may be less conspicuous, thereby less susceptible to natural enemy attack; thus, there may be no significant benefit to laying them on the lower surface or covering them with abdominal scales.

Pistia stratiotes plants may have as many as 16 leaves at one time during the summer and each leaf may last about 35 days (Dewald and Lounibos 1990, Dray and Center 1993). Even though the nutritional quality of the leaf decreases as it ages, 35 days should be sufficient time for the completion of larval development within the natal leaf even in those of

the poorest quality. However, if larval development begins in intermediate position leaves (e.g., position 5-8) of low nutrient levels, it is conceivable that there may be insufficient time to complete larval development before the leaves begin to sink and decay. Thus, it was surprising that more eggs were not laid on the inner leaves. The effect of limited leaf availability could be further exaggerated if the plant increases the rate of leaf decay in those leaves that are fed upon, as shown with another aquatic plant species (Juliano 1988).

The results of this study suggest that other selective forces, such as allelochemicals or natural enemies, may decrease survival in larvae consuming these inner leaves. However, this study also suggests that leaves 1-4 were non-toxic to these larvae as they were successfully reared on these leaves during this (Chapter 3) and other studies. Several species of parasitic insects are known to forage in *P. stratiotes* plants and parasitize over 50 percent of the larvae of another lepidopteran, *S. multiplicalis* (Knopf and Habeck 1976). The susceptibility of *S. pectinicornis* to these natural enemies has yet to be determined. Possibly the dense pubescence of the inner-most leaves presents a greater physical barrier to leaf penetration by the early instars compared with the relatively less dense pubescence of the outer leaves. Moreover, although increased risk from natural enemies may result, larvae may move to different leaves or plants during their development. Therefore, there appear to be many factors that have been selected for the placement of egg masses and solitary eggs on *P. stratiotes* leaves. Among the most important may be the dynamics of plant quality, leaf availability, mortality due to natural enemies, and desiccation.

Insects can respond to the deterioration in host quality by adaptively changing their population structure such as producing migratory forms. This phenomenon has been well documented in species or stages of species that have a limited ability to disperse and include aphids (Dixon 1985), a planthopper (Denno and Grissell 1979), and several lepidopteran species that are able to oviposit on plant species (Wiklund 1975, Craig, Itami, and Price 1989) or individuals (Leather 1985) that have the greatest selective advantage for their offspring. Although the influence of host quality on such changes in population structure of this species have yet to be determined, the influence of host quality on the location of egg masses and solitary eggs was tested. This study did not find any indication of oviposition preference for the most nutritious leaves whether the larvae were reared on high or low quality plants. The only significant influence of fertilizer on egg mass location was a higher percentage of the egg masses produced from the high treatment females laid on leaf positions 9-12. Therefore, host quality is important for the growth and development of larvae, yet it is not the only factor involved in oviposition preference of this species.

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REPORT DOCUMENTATION PAGE

Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503.

1. AGENCY USE ONLY *(Leave blank)*	2. REPORT DATE September 1998	3. REPORT TYPE AND DATES COVERED Final report

4. TITLE AND SUBTITLE
Influence of *Pistia stratiotes* Plant Quality on Fecundity and Egg Distribution of the Biological Control Agent *Spodoptera pectinicornis*

5. FUNDING NUMBERS

6. AUTHOR(S)
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7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
U.S. Department of Agriculture, Agriculture Research and Education Service,
3205 College Avenue, Fort Lauderdale, FL 33314

8. PERFORMING ORGANIZATION REPORT NUMBER
Technical Report A-98-4

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
U.S. Army Corps of Engineers, Washington, DC 20314-1000;
U.S. Army Engineer Waterways Experiment Station,
3909 Halls Ferry Road, Vicksburg, MS 39180-6199

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES
Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

12a. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution is unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT *(Maximum 200 words)*

The potential fecundity of an insect may be influenced by the quality of the larval diet. Moreover, the distribution of eggs on the leaf surface may determine the success of that species colonizing the plant. This study determined the influence of larval host quality of the aquatic weed *Pistia stratiotes* on the fecundity and egg distribution of the biological control agent *Spodoptera pectinicornis*.

Plants were grown with relatively low and high levels of N:P:K fertilizer. The results indicated that all three elements were higher overall in the high treatment and that nitrogen and potassium levels decreased in the high treatments from the inner to the outer leaves. The phosphorus and potassium levels increased in the low fertilizer treatment from the inner to the outer leaves.

Female and male pupal biomass was significantly greater in the high fertilized treatments. Adult females that emerged from larvae fed the low fertilizer treatment lived 4.6 days or about one day longer than those from the high treatment. Most of the eggs were laid in egg masses, while overall about 12 percent were laid as solitary eggs. A significantly greater percentage of solitary eggs were laid by females from the low fertilizer treatment (17.3 ± 3.4 percent) compared with those from the high

(Continued)

14. SUBJECT TERMS

Biological control of weeds	Nitrogen	Potassium
Fecundity	*Pistia stratiotes*	Oviposition preference
Host plant quality	Phosphorous	*Spodoptera pectinicornis*

15. NUMBER OF PAGES
27

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
UNCLASSIFIED	UNCLASSIFIED		

NSN 7540-01-280-5500

Standard Form 298 (Rev. 2-89)
Prescribed by ANSI Std. Z39-18
298-102

13. (Concluded).

fertilizer treatment (8.3 ± 2.3 percent). Total fecundity was greater ($P = 0.15$) in the high fertilizer treatment. Females that emerged from larger pupae, regardless of larval diet, produced significantly more eggs.

Most of the egg masses were laid on the lower surface of leaves, on leaf positions 5-8 (counting from the young inner to the outer leaves) and on days 1 and 2. Leaf position and day significantly influenced solitary egg position, where more eggs were found on leaves 1-8 during days 1-4. The results suggest that high-quality larval diet increases adult fecundity and that the distribution of eggs are influenced by the biological constraints of host leaf dynamics, declining leaf quality, and potential threat of natural enemies.